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ANATOMY OF THE PRIMARY AXIS
OF SOLANUM MELONGENA

A DISSERTATION SUBMITTED TO THE
GRADUATE FACULTY IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
ALBERT FREDERICK THIEL

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ANATOMY OF THE PRIMARY AXIS OF SOLANUM MELONGENA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 426

ALBERT F. THIEL

(WITH TEN FIGURES)

Introduction

The eggplant, *Solanum melongena*, is grown as a truck crop in Florida, Louisiana, California, Virginia, New Jersey, and a few northern states. Because of its increasing commercial value and its importance as a food, some interest has developed as to its anatomy. Although the anatomy of closely related species in the Solanaceae has been investigated rather completely in some cases, the writer was unable to find any literature on the anatomy of this plant.

HARTIG (7) was the first to discover the bicollateral condition in plants, and HANSTEIN (6) first reported internal phloem in the Solanaceae. Since the bicollateral condition was first reported, investigators have found the same condition in eighteen families. HOLROYD (9) calls attention to the fact that "This advanced developmental condition is rare in the primitive cotyledons or Incompletae (Apetalae); is more frequent in the Apopetalae (Polypetalae); and most frequent, as well as most perfectly evolved, in the Sympetalae."

GERARD (5) described the transition from root to stem in *Cucumis melo* and *Cucurbita maxima*. He concluded that the internal phloem is merely a part of the external that is reoriented on the inner face of the bundle. HERAIL (8) studied the comparative anatomy of the stem of many dicotyledons, and concluded that the Cucurbitaceae alone possess a true bicollateral bundle. SCOTT and BREBNER (12), in their studies on *Thladiantha dubia*, found that the internal phloem connects with the external in the medullary ray. They found that during transition from stem to root the internal phloem passes out and unites with the external phloem.

FISCHER (4), studying the hypocotyl of *Cucurbita pepo*, found that the inner phloem gradually died out, ending blindly below. LA-

MOUNETTE (11) found no communication between external and internal phloem in *C. maxima*, and concluded that the development of internal phloem is an abnormal formation due to the activity of certain pith cells. VON FABER (14) traced the development of the bundles in the stem of *C. pepo*, and concluded that the internal phloem arises very early at the growing point. He found that both inner and outer phloem existed before any vessels were formed, and that the sieve tubes of the inner phloem originated from the same procambial strand as the rest of the bundle. WORSDELL (15) investigated the medullary phloem in the Cucurbitaceae, and concluded that it represents "a vestigial structure, the remnant of a former system of medullary vascular bundles in which the xylem has disappeared."

Mrs. SMITH (13), studying the development of *Dionaea muscipula*, reports that there is no transition in the hypocotyl. She states that the bundles are inverted as they leave the cotyledons.

ARTSCHWAGER (1), in his work on the anatomy of the potato, studied the root-stem transition, and states: "In the change from the exarch to the endarch condition it is noticed first, that the two protoxylem groups of a diarch root begin to swing outward, one following a left, the other a right curve." At a point just below the cotyledons he found that the primary xylem groups, instead of forming a radial row, come to lie in a tangential plane. The change from the exarch to the endarch condition was completed in the region above the cotyledons. With reference to the origin of the internal phloem, he concluded that it belongs to the stele proper and does not represent the vestigial remains of a secondary set of bundles. He found the first change in the primary phloem to be a breaking up of the two phloem groups with the formation of three or four smaller groups. These smaller groups orient themselves in such a way that two or three of them come to lie in the center of the stem, between the separating xylem strands. The other phloem groups take a position at the periphery of the stele.

Miss KING (10) traced the course of the bundles from root to stem in *Lycopersicum esculentum*, and found that the primary xylem plate differentiates into two distinct bundles. The metaxylem differentiates tangentially toward the periphery of the stele at successively higher levels. She found that the protoxylem maintained its

original position until the level just below the cotyledonary plate was reached. Centripetal differentiation of the protoxylem began at this point and continued until the primary xylem groups were almost endarch at the cotyledonary plate. With respect to the primary phloem, she found that it divided into smaller groups, and that strands differentiating toward the center constituted the internal phloem. The external phloem formed four equally distributed groups, which were oriented collaterally at the outer face of the xylem groups. Simultaneously the internal phloem formed two groups located at the inner limits of the primary xylem, thus establishing the bicollateral condition.

The investigations on the potato by ARTSCHWAGER, and on the tomato by Miss KING, show some variation in the method of transition in closely related species. Neither of these workers investigated the possibility of changes occurring in the petiole and midrib of the cotyledon. It was the purpose of this study to investigate the ontogeny of the root, the root-stem transition in the axis, and the vascular anatomy of the cotyledons.

Material and methods

The seed used is commonly known as the Black Beauty variety. BAILEY (2) classifies this variety as *Solanum melongena* L. var. *depressum* Bailey. The plants were grown in the greenhouse, and seedlings of different ages were used in the investigation. The 5-day-old seedlings furnished the best material for the study of root-stem transition, because at this age the primary body was fully differentiated and there was little or no development of secondary thickening due to cambial activity. Several killing agents were used, but the best results were obtained with Flemming's weaker solution. The usual laboratory methods of dehydrating and imbedding in paraffin were followed. The sections were cut to a thickness varying from 7 μ in the young root to 15 μ in the hypocotyl, and were stained with the triple stain of safranin, gentian violet, and orange.

Gross morphology

The ovules of *Solanum melongena* are campylotropous, and the cotyledons within the seed coats are erect with reference to the axis of the embryo. When proper conditions are provided, active germi-

nation begins in about four days. As a result of the absorption of water, the seed coat is split near the micropylar end. The hypocotyl emerges first through the split end, turning downward and differentiating the primary root. By further growth the hypocotyl partially withdraws the cotyledons from the seed coat, forming an arch, which straightens out by differential growth after it emerges from the soil. The seed coat adheres to the cotyledons for a few days, eventually falling to the ground. The 5-day-old seedling has a primary root approximately 4 cm. long, a hypocotyl 2 cm. long, and two cotyledons 1 cm. in length. The hypocotyl grows more rapidly than the epicotyl in the early stages of development, and the cotyledons are therefore the main photosynthetic organs during this early period.

The Black Beauty variety is a small and straggling plant, many of the branches finally resting on the ground. The pubescent leaves are alternate, simple, lobed, oblong, oval or ovate, unequal at the base, acute at the apex, and varying from 2 to 6 inches in length.

Ontogeny of root

Studies on the development of the primary structures were made with young roots 3 cm. in length. Transverse and longitudinal sections were made from the growing point to the region of maturation of the primary tissues. At the growing point the entire axis is promeristem. The cells are essentially isodiametric and alike; their walls are thin and without pits. The nuclei of the cells are large and the protoplasm is extremely dense, while vacuoles and intercellular spaces are absent. The primary meristems originating from the promeristem are not sharply marked. At about 5 mm. from the growing point, the regions of the stele, cortex, and epidermis are clearly distinguishable. The epidermal and cortical cells are clearly delimited, while most of the cells of the stele are still undifferentiated. Two glands are noticeable in the region of the pericycle. They appear before any protoxylem or protophloem cells are differentiated, and predesignate the location of these elements. They lie in the pericycle opposite the protophloem cells, and may be similar to the "sap-passages" mentioned by DEBARY (3) in the pericycle of primary tissues of the roots of the Umbelliferae. At a higher level, as the primary tissues reach maturation, these glands seem to be absorbed.

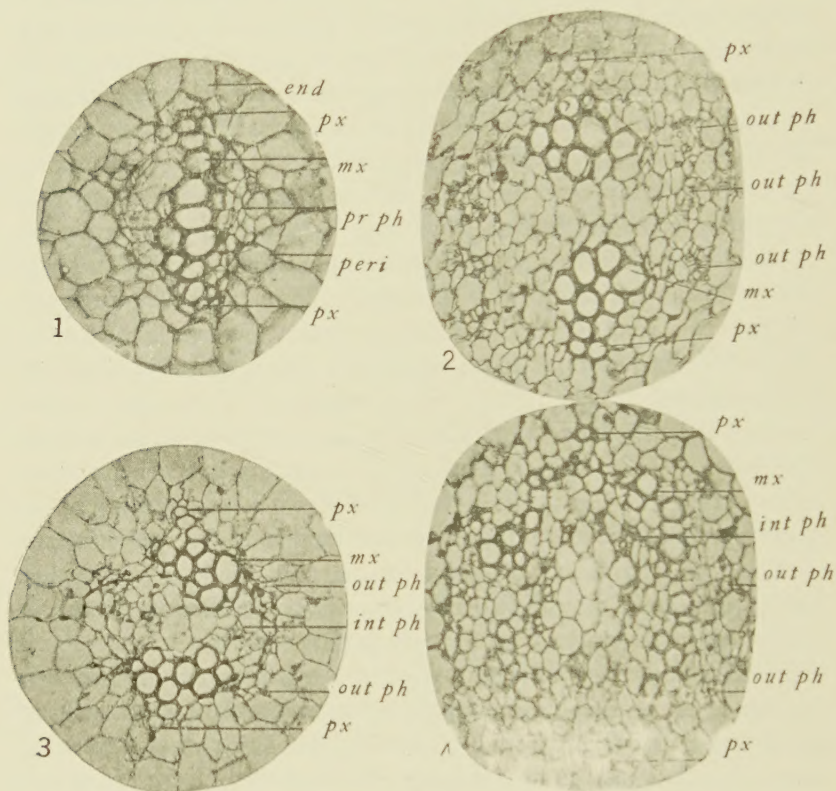
The epidermis and cortex are the first to differentiate from the primary meristems. The epidermis consists of a single layer of cells, greater in their vertical than in their radial dimension. Root hairs are numerous just beyond the region of elongation. The cortex surrounds the stele, and consists of a layer of parenchyma six cells in thickness. Its cells are arranged loosely and are much longer in their vertical than in their radial diameter. Large intercellular spaces are noticeable. The endodermis is composed of one layer of cells and is the innermost layer of the cortex. Its cells are somewhat longer, as seen in longitudinal section, than those of the pericycle, and their vertical dimension much exceeds the radial. The Casparian strips can be recognized at about 1 cm. above the root tip. The pericycle consists of a single layer of parenchymatous cells, and lies between the endodermis and the primary phloem. The protoxylem abuts directly against it. The cells of the pericycle are also longer in their vertical than in their radial diameter. Lateral roots originate from the pericycle cells, either opposite or at a slight tangent to the protoxylem points. A few of these were first observed at a time approximately coincident with maturation of the primary xylem elements.

The stele is a diarch, radial protostele (fig. 1). The protoxylem and protophloem are differentiated from the procambium simultaneously, development in both cases being exarch. The protoxylem is composed of long, slender, annular and spiral tracheae. The first vessels of the metaxylem to appear are the scalariform tracheae, and these are followed by reticulated and pitted tracheae. Parenchymatous cells separate the primary phloem groups from the diarch primary xylem plate. The protophloem is composed of elongated parenchymatous cells; the metaphloem, of sieve tubes, companion cells, and phloem parenchyma.

Root-stem transition

In studying the changes involved in passing from a diarch, radial protostele of the root to the bicollateral type of bundles in the cotyledons and stem, 5-day-old seedlings were used. At this age the hypocotyl was 2 cm. long and the cotyledons 1 cm. in length. In order to be certain of the exact location of the protoxylem points in the various sections with reference to the divergence of the cotyledons, whole

seedlings were used. By following this method the protoxylem points were always oriented in the same position on the slides, and less diffi-



FIGS. 1-4.*—Fig. 1, transverse section of root showing primary tissues of stele, $\times 510$; fig. 2, transverse section of hypocotyl showing breaking up of diarch xylem plate and primary phloem groups, $\times 460$; fig. 3, same at somewhat higher level, showing beginning of bifurcation of metaxylem and inward differentiation of phloem, $\times 400$; fig. 4, transverse section of hypocotyl showing complete bifurcation of metaxylem and numerous internal phloem groups, $\times 490$.

*Abbreviations for all figures: *end*, endodermis; *epi*, epidermis; *gr.pl*, growing point of stem axis; *int.ph*, internal phloem; *mx*, metaxylem; *out.ph*, outer phloem; *peri*, pericycle; *pr.ph*, primary phloem; *px*, protoxylem.

culty was experienced in following the changes taking place in the serial sections.

The first indication of a change from the exarch condition begins very low in the hypocotyl, occurring approximately 2.25 cm. below

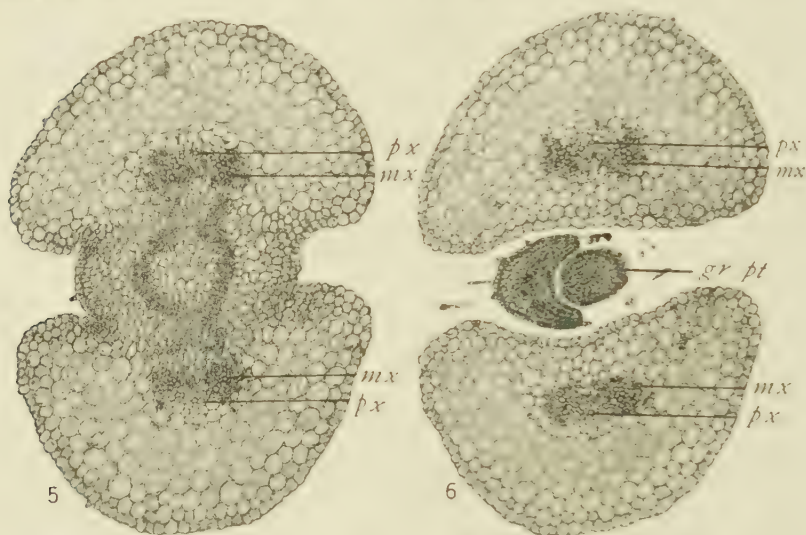
the cotyledons. All investigators to date report transition to be completed, either in the hypocotyl or stem axis; but in *Solanum melongena* it is completed in the bundles of the midrib of the cotyledons. The first change noted is a breaking up of the diarch xylem plate, forming two units of the primary xylem elements (figs. 1, 2). The cells in the central portion of the stele fail to differentiate as tracheae but remain parenchymatous. Simultaneously the two primary phloem groups each divide into three distinct groups (fig. 2). There is no indication at this level of an internal phloem. At a slightly higher level there is a bifurcation of the metaxylem of the two primary xylem units (figs. 3, 4). At this level there is a lateral rather than a centripetal differentiation of the metaxylem. The central group of phloem cells shown in fig. 2 are nearer to the center of the axis at the level shown in fig. 3. This inward differentiation from both sides continues until there are numerous small groups formed by further division of the original phloem groups (fig. 4). Each of the four remaining groups of the primary phloem lying nearest to the metaxylem are gradually inclined in a tangential direction toward the position of the protoxylem points.

At the level just below the cotyledonary plate the position of the protoxylem remains unchanged. The metaxylem of the two units has taken a position close to the periphery of the stele. The phloem groups are placed on both sides of the metaxylem, so that four tangentially oriented groups of primary xylem are differentiated, forming four bicollateral transition bundles. It should be noted, however, that at this level there is no outer phloem lying directly outside of the protoxylem elements.

Near the cotyledonary plate there is a gradual separation of the two double bundles formed by the breaking of the original diarch xylem plate and the reorientation of the phloem and metaxylem just described. One of these double units, consisting of one protoxylem point and its metaxylem, together with the internal and outer phloem groups, becomes the vascular trace of one of the cotyledons; and the second unit, that of the other. The protoxylem points have begun to change their position just below the cotyledonary plate, and at successively higher levels there is a gradual centripetal differentiation of the protoxylem and a centrifugal differentiation of the

metaxylem; but the endarch condition is not finally attained in the hypocotyl (fig. 5).

At the cotyledonary plate the direction of development of the primary xylem is still tangentially exarch (fig. 5), and there are numerous groups of internal phloem on the inner faces of the protoxylem and metaxylem elements. The outer phloem, however, is present only on the outer faces of the metaxylem groups (fig. 5). At a slightly

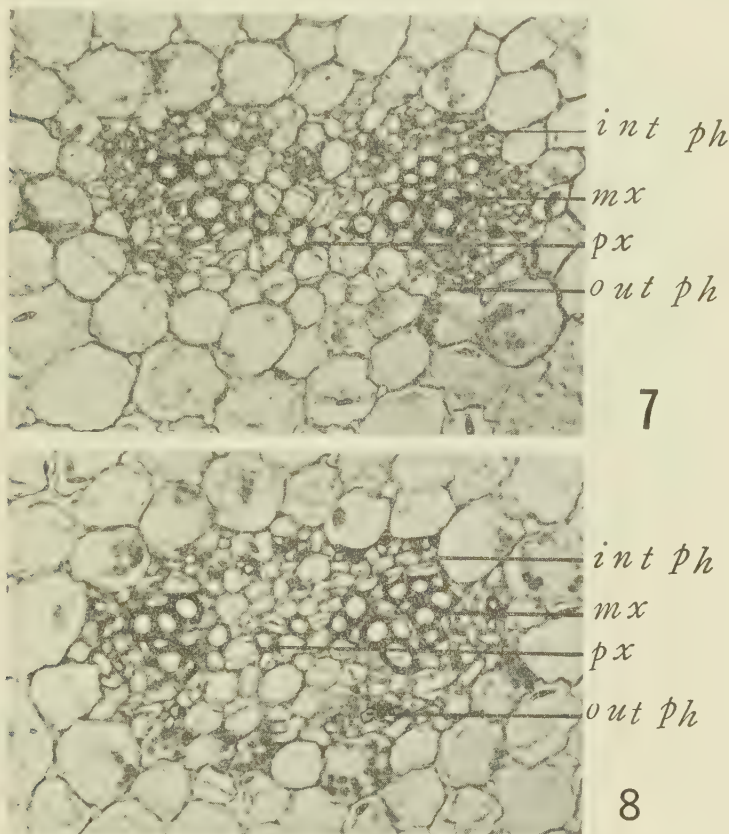


FIGS. 5, 6.—Fig. 5, transverse section through cotyledonary plate, showing complete separation of two units of original diarch xylem plate, each unit consisting of protoxylem with its bifurcated metaxylem together with internal and outer phloem groups, $\times 150$; fig. 6, transverse section through petiole of cotyledons 1 mm. above cotyledonary plate; primary xylem elements still exarch.

higher level, where there is complete divergence of the cotyledons, the same situation obtains with respect to the phloem in the cotyledonary petioles (fig. 6). The protoxylem and metaxylem are shifting their position; however, the former is developing adaxially with reference to the upper surface of the petiole, and the latter, abaxially.

The transition beyond the cotyledonary plate was followed in the petiole and midrib of one of the cotyledons (the illustrations are oriented so that the adaxial surface of the petiole and lamina are toward the top of the page). At successively higher levels the change

from the exarch to the endarch condition is accomplished gradually (figs. 7-10). The protoxylem differentiates adaxially, and finally assumes a position nearer to the upper epidermis than the metaxylem-

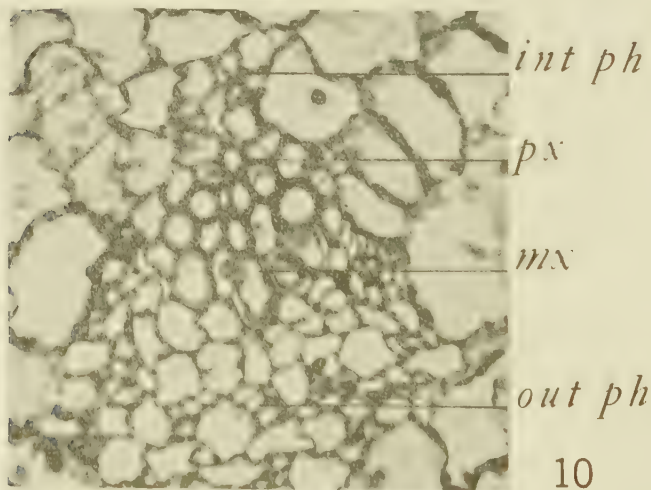
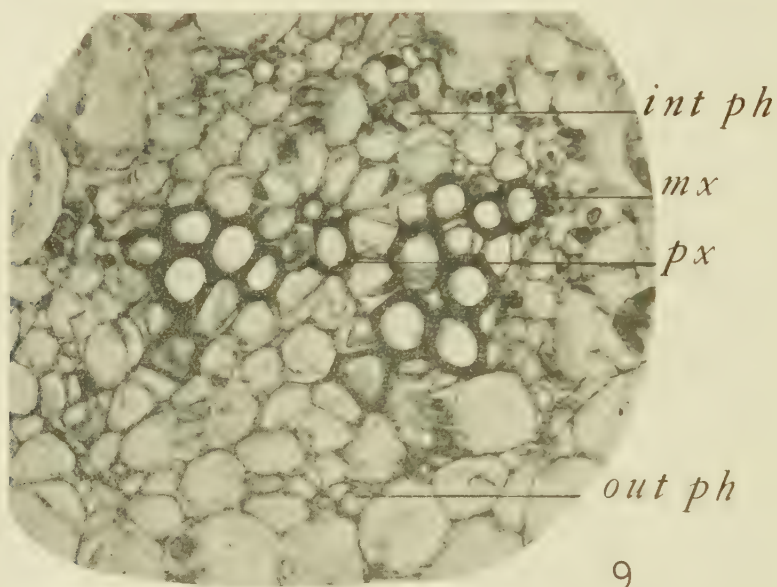


FIGS. 7, 8.—Transverse sections through petiole and lamina of cotyledon at successively higher levels; protoxylem differentiates adaxially and metaxylem abaxially until endarch condition is established (adaxial surface of petiole and lamina toward top of page).

lem. At the same time the metaxylem differentiates abaxially until the endarch condition is completely established (figs. 9, 10).

The internal phloem groups are numerous in the hypocotyl and petiole of the cotyledon. These groups gradually decrease in number in the bundle of the midrib until only one group remains opposite

the inner face of the protoxylem (figs. 9, 10). The outer phloem, lying opposite the outer faces of the two metaxylem groups, differ-



FIGS. 9, 10.—Transverse sections through petiolar bundle at still higher levels in which endarch condition is established (adaxial surface of petiole and lamina toward top of page).

entiate toward the position originally occupied by the protoxylem point. These outer phloem groups are best illustrated in fig. 9. It will be noted that they incline progressively nearer one another until there is complete union of the two groups. The bicollateral condition is thus established.

The foliar traces in the first internode are completely endarch, and differentiate against the vascular elements of the hypocotyl slightly below the cotyledonary plate.

Discussion

The method of root-stem transition in *Solanum melongena* agrees in general with the findings of Miss KING for the tomato. She did not follow the transition into the cotyledon, but found it almost completed at the cotyledonary plate. At this level in *S. melongena* the development of the primary xylem is still tangentially exarch. Her findings with respect to the behavior of the primary phloem groups in the tomato agree with the results of the writer. In working with the potato, ARTSCHWAGER found that the two primary xylem groups begin to swing outward, "one following a left, the other a right curve." The writer found no suggestion of this method in *S. melongena*. Instead of the two primary xylem groups following different curves, there was a bifurcation of the metaxylem. ARTSCHWAGER's findings with respect to the phloem agree with those of the writer.

With respect to the origin of the internal phloem, the writer agrees with those investigators who believe that the internal phloem passes out and unites with the external phloem in the root.

Summary

1. In *Solanum melongena*, the primary meristems, calyptrogen, dermatogen, plerome, and periblem originating from the promeristem are not clearly differentiated.
2. The epidermis consists of one layer of cells from which root hairs arise; the cortex consists of six layers of parenchyma cells; and the endodermis and pericycle each consist of one layer. Lateral roots originate from the cells of the pericycle.
3. The stele of the primary root is a diarch, radial protostele.

4. Root-stem transition begins very low in the hypocotyl. The first change noted is a breaking up of the diarch xylem plate and the two primary phloem groups, forming two units of the primary xylem and phloem. At a higher level there is a bifurcation of the metaxylem and an inward differentiation of two of the phloem groups.

5. Near the cotyledonary plate there is a separation of the two double bundles formed by the breaking of the original diarch xylem plate. One of these double units becomes the vascular trace of one of the cotyledons, and the second unit, that of the other.

6. By inward differentiation and further division, several small primary phloem groups finally come to lie opposite the inner faces of the primary xylem elements. The four remaining groups lying nearest to the metaxylem are gradually inclined in a tangential direction, eventually lying on the outside of the original position of the protoxylem points. This development continues until the bicollateral condition is established.

7. The endarch condition is not attained in the hypocotyl but in the midrib of the cotyledon.

8. The foliar traces in the first internode are completely endarch, and differentiate against the vascular elements of the hypocotyl slightly below the cotyledonary plate.

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